ORIGINAL ARTICLE

Werner Ulrich

Decomposing the process of species accumulation into area dependent and time dependent parts

Abstract In 1960, Preston predicted that the process of species accumulation in time (species–time relationship, STR) should be similar to the species–area relationship (SAR) and follow a power function with a slope of about 0.26. Here these two conjectures are tested using data of the spatiotemporal species accumulation in a local community of beech forest Hymenoptera. A power function species–area–time model of the form $S = S_0 A^z t^\tau$ gave better fits to observed species numbers than a simple power function SAR model, and was able to predict similar species turnover rates (about 9% per year) to those inferred by other methods. The STR was well fitted by a power function, although due the limited time span (8 years) a logarithmic STR pattern cannot be ruled out. STR slopes ranged between 0.01 and 0.23 and were lower than predicted by Preston. Temporal species turnover appeared to be negatively correlated to species densities and positively correlated to species body weights. Ecological guild and taxon membership did not significantly influence temporal species turnover.

Keywords Beech forest · Hymenoptera · Parasitoids · Species–area relationship · Species–time relationship · STAR model

Introduction

The study of species–area relationships (SARs) has a long tradition in ecology (Arrhenius 1921; Gleason 1922; Rosenzweig 1995; Lomolino 2000; Hubbell 2001; Lennon et al. 2001; Scheiner 2003; Tjørve 2003). Theoretical (Carlson and Doyle 1999; Harte et al. 1999; Hubbell 2001) and empirical (Preston 1960; Connor and McCoy

1979; Williamson 1988; Rosenzweig 1995; Fridley et al. 2005) studies showed that SARs can be most often modelled by a power function of the type

$$S = S_0 A^z, \tag{1}$$

where S denotes the number of species in a given area A. S_0 and z are the parameters of the model with S_0 being an estimate of the mean number of species per unit area. Additionally, SARs were found to be triphasic, having different slopes z at local, regional and intercontinental scales (Preston 1960; Shmida and Wilson 1985; Rosenzweig 1995; Fridley et al. 2005).

However, time and area act closely together in the process of species accumulation. Data for many SARs (especially those inferred from atlas studies) were obtained over longer time periods (e.g., Judas 1988; Davies and Spencer Smith 1997; Ulrich and Buszko 2003a, b). Hence, published SARs based on medium to long-term data sets contain an additional temporal species turnover factor that might obscure the actual SAR pattern. This might result, for instance, in deviations from predicted power function SAR patterns and in higher slopes than expected from a pure SAR (Adler and Lauenroth 2003). Nevertheless, the temporal equivalent to the SAR, the species–time relationship (STR), has received much less interest (Adler 2004; Maurer and McGill 2004; Adler et al. 2005). This is surely caused by the lack of appropriate long-term data sets necessary for analyzing patterns of species accumulation in time. It was Preston (1960) who hypothesized that STRs should have similar shapes to SARs. His argument invokes two hypotheses. First, STRs should follow power functions, and second, the slope z should be similar to the slopes typical for SARs. Preston's first conjecture is generally supported by the few available data sets. Preston (1948, 1960), Rosenzweig (1995, 1998), Hadley and Maurer (2001), Adler and Lauenroth (2003), and Adler et al. (2005) reported power function STRs at small to intermediate time scales. Jaquemyn et al. (2001) fitted a logarithmic STR model to their data on forest species numbers. The results of Adler and Lauenroth (2003) and

W. Ulrich
Department of Animal Ecology, Nicolaus Copernicus University in Toruń, Gagarina 9, 87-100 Toruń, Poland
E-mail: ulrichw@uni.torun.pl
Tel.: +48-56-6114469

White ([2004](#)) also point to a two-phase STR pattern at small to intermediate time scales similar to those for SARs. However, Adler and Lauenroth ([2003](#)) found, at least for grasslands, higher slope values of STRs in comparison to respective SAR slopes. This contradicts Preston's second conjecture.

The starting point for a general species–area–time relationship (STAR) can be based on three assumptions. The first assumption holds that species numbers are proportional to a time and to an area dependent function. Under this assumption, S will be the product of the area and the time dependent terms:

$$S = f(A)g(t). \tag{2}$$

Second, the area dependent function $f(A)$ is assumed to be of the power function type. Third, according to Preston's conjecture $f(t)$ should also be of the power function type resulting in

$$S = S_0 A^z t^\tau. \tag{3}$$

For $t = 1$ (1 year considered) Eq. 2 reduces to a simple SAR. τ denotes the STR slope parameter. Plots of S/t^τ against A and $S/S_0 A^z$ against t give time and area corrected SAR and STR patterns.

This model should do best at the regional scale where SARs and STR are expected to follow power functions (Rosenzweig [1995](#), [1998)](#). However, at the local habitat scale the influence of time might be even more pronounced due to the higher temporal rates of species turnover (Ulrich [2001a](#); Ulrich and Ollik [2004](#)). Further SARs and STRs do not necessary follow power functions (Scheiner [2003](#); Tjørve [2003](#)). The present study therefore aims to test whether the STAR model of Eq. 3 is able to separate time and area effects in the accumulation of species at the local scale.

Materials and methods

The present study is based on data about local densities and species numbers of Hymenoptera obtained in a long-term quantitative sampling program for estimating arthropod densities and biomasses in a beech forest (Melico-Fagetum; Subass. *Lathyrus vernus*) on limestone near Göttingen (northern Germany) (Schaefer [1996](#), [1999](#); Ulrich [2001b](#)). Between 1980 and 1987, a total of 109 m^2 of forest floor within a study site of about 1 ha was quantitatively sampled with 1 (1980), 12 (1981), 12 (1982), 16, (1983), and 20 (1984, 1985, 1986, 1987) emergence traps (ground photo eclectors; Funke [1971](#)) that covered 0.25 m^2 (1984, 1985) and 1 m^2 of forest floor each. Emergence traps sample positive phototactive insects (like Hymenoptera) that emerged under the trap. In 1981, 10 additional traps covered 1.8 m^2 each. Hence, the present study is based on a total of 131 traps that were installed during 8 years of study to allow for a repeated sampling of the same part of the forest. These traps operated from March to December and were checked weekly. Picric acid was used as the killing liquid. A detailed description of the sampling program as well as an ecological classification of each species is contained in Ulrich ([1998](#), [2001a)](#). In total, 32,184 individuals of 598 hymenopteran species were caught with these traps.

Local species accumulation curves (SACs) were constructed by a random combination of traps. Because of the small total study area, spatial species turnover according to Rosenzweig ([1995](#)) should not influence the results. Therefore, the combination of traps did not consider trap distances. Each data point of the SACs below therefore represents the total number of species trapped with a random combination of 1–131 traps and covering 1–109 m^2 forest floor and 1–8 study years (sampling with replacement). These SACs therefore contain a spatial (the SAR) and a temporal (the STR) component. To avoid statistical problems stemming from an unequal number of data points along the area–time gradient, 10 random combinations each for areas of 1–10, 11–20,..., 101–109 m^2 were taken. Each species accumulation curve was therefore based on 110 data points. The study time t for each data point was the total time difference for the given combination of traps from different study years.

Species accumulation curves were separately constructed for all Hymenoptera and for those subtaxa (Ichneumonidae, Braconidae, Chalcidoidea, Proctotrupoidea, and Ceraphronoidea) and guilds (parasitoids of miners, gall-makers, ectophytophages, saprophages, mycetophages, predators, and egg parasitoids) that contained more than 30 species in the forest. The classification into ecological guilds is the same as in Ulrich ([1998](#), [1999a](#), [2001a)](#).

The power function STAR model was fitted to these SACs using the non-linear estimation module (Levenberg–Marquardt procedure) of Statistica 7 (Statsoft [2005](#)). Kolmogorov–Smirnov tests were used to assess the goodness of fit.

Results

The simple area dependent SAC of the forest Hymenoptera was best fitted by a power function model with an expected mean of 60 species per m^2 (the species density) and a slope of 0.50 ($R^2 = 0.98$; Fig. [1](#)a). The observed species density, however, was 71 (Ulrich [1999b](#), [2001b)](#). Using non-parametric jackknife and parametric curve-fitting methods, Ulrich ([1999b](#)) estimated the yearly number of species on the study area at between 350 and 500. The simple SAC model of Eq. 1 overestimated species numbers at areas above 80 m^2 and predicts more than 600 species at 100 m^2. The more pronounced curvature of the SAC with respect to model prediction, however, caused the best fitting power function to underestimate species numbers at intermediate sample areas (Fig. [1](#)a). For comparison, I also
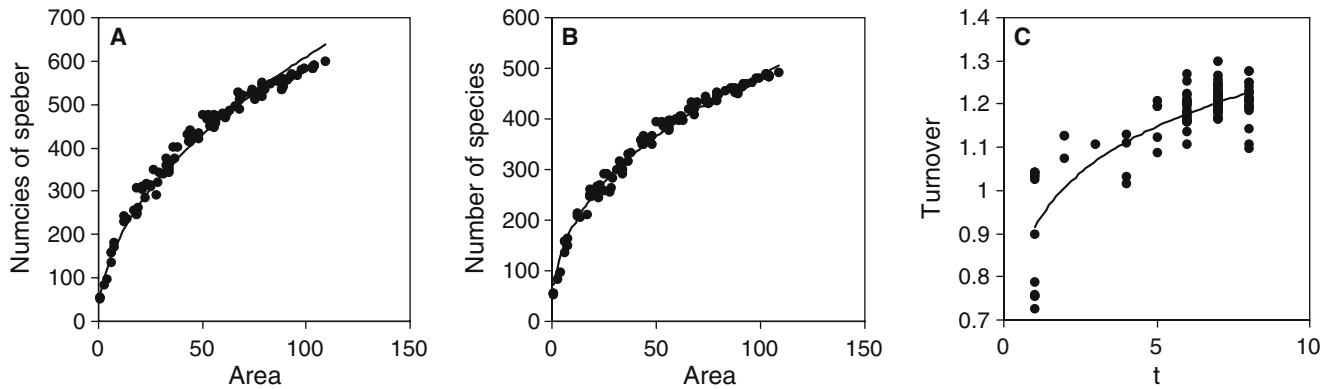
Fig. 1 a SAC as dependent on area of all beech forest Hymenoptera. The best fit power function SAC model in **a** significantly overestimates species numbers at sample areas above 80 m² and underestimates species numbers at areas between 10 and 80 m² ($P(\chi^2) = 0.78$). **b** The correction of the SAC by dividing through the time dependent term of the STAR model (Eq. 3) significantly improves the fit of the power function SAR model ($P(\chi^2) < 0.01$). **c** The correction for area resulted (Eq. 3) in a significant correlation (Spearman' $R = 0.62$; $P < 0.001$) between species accumulation in time (turnover) and study time. **a** $S = (75.0 \pm 2.1) A^{(0.45 \pm 0.01)}$; $R^2 = 0.98$. **b** $S = 73 A^{0.41}$; $R^2 = 0.99$. **c** Turnover $= t^{0.094}$; $R^2 = 0.68$. All regression parameters are significant at $P < 0.001$. Complete STAR model: $S = (73.0 \pm 1.7) A^{(0.41 \pm 0.01)} t^{(0.094 \pm 0.01)}$; $R^2 = 0.99$

fitted a logarithmic SAC model ($S = z \ln(A) + S_0$; Gleason [1922](https://doi.org/)). The fit of this model was worse ($R^2 = 0.93$), underestimated species numbers above 50 m² due to its stronger curvature, and predicted a negative species density ($S = 136 \ln(A) - 81$). Hence, the present paper concentrates mainly on the power function model.

Fitting the power function STAR model of Eq. 3 ($S = (73 \pm 1.7) A^{(0.41 \pm 0.01)} t^{(0.094 \pm 0.01)}$) to the data significantly improved the fit (Fig. 1b, Table 1). The plot of study time corrected species numbers versus time was closely fitted by the power function SAR. The new model correctly predicted mean species numbers per square meter ($S_0 = 73 \pm 2$) and species numbers over its entire range. The estimate of 485 species at 100 m² lies within the boundaries of previous estimates (350–500 species; Ulrich 1999b, 2001b). The correction for area resulted in a significant species number–time relationship (Fig. 1c).

Even for the short study period of only 8 years most τ-values of the study time term (Eq. 3) differed significantly from zero (Table 2) and ranged between 0.05 and 0.17 for the taxa and 0.01 and 0.23 for the guilds. The highest τ-values are predicted for Braconidae ($\tau = 0.14$) and Ceraphronoidea ($\tau = 0.17$), and for the parasitoids of ectophytophagous insects ($\tau = 0.13$) and sap-suckers ($\tau = 0.23$).

The τ-values allow for the prediction of annual species turnover rates. From $S = t^{\tau}$ we get, for consecutive years for all Hymenoptera, $S = 2^{0.094} = 1.067$. Hence the annual turnover rate is expected to be 6.7%. This fits into previous density fluctuation based estimates of Ulrich (2001b) of 5–15% annual species turnover. The STAR model predicts the highest turnover rates for Braconidae (10%) and Ceraphronoidea (13%) and for parasitoids of sapsuckers (17%). The lowest annual turnover rates are predicted for Chalcidoidea and for the egg-parasitoids (Table 3).

The τ-values (and therefore annual turnover rates) were neither correlated with species numbers per taxon or guild nor with mean densities or temporal variability in density (all significance values of Spearman's rank order correlations > 0.1). However, there was a strong effect of body weight on the model parameters z and τ (Figs. 2, 3). The computation of species accumulation curves for binary weight classes (octaves) showed that the slope of the simple SAC increased with body weight (Fig. 2a). The STAR model allowed for the decomposition of this increase into an area (Fig. 2b) and a study time dependent component (Fig. 2b). Both components were highly significant ($P(t) < 0.001$). The τ-values of Fig. 2c predict, for the lower weight classes, annual species turnover rates of about 4% ($2^{0.06} = 1.042$) and,

Table 1 Test values of the Kolmogorov–Smirnov test of fits of the simple power function SAR model, and the power function STAR model (Eq. 3) to species numbers of hymenopteran taxa and guilds

	SAC K–S value	STAR K–S value
Taxon		
Ichneumonidae	0.043	0.009
Braconidae	0.018	0.009
Chalcidoidea	0.014	0.004
Proctotrupoidea	0.009	0.007
Scelionoidea	0.036	0.010
Ceraphronoidea	0.029	0.010
All Hymenoptera	0.016	0.005
Guild		
Miners	0.020	0.003
Gall makers	0.018	0.002
Ectophytophages	0.034	0.002
Sap suckers	0.024	0.020
Saprophages	0.006	0.004
Mycetophages	0.041	0.007
Predators	0.032	0.009
Egg parasitoids	0.034	0.008

Higher test values point to a worse fit. The critical K–S value for $n = 109$ at $P = 0.05$ is 0.129

Table 2 Hymenopteran taxa and guilds: simple SAC slopes (Eq. 1) slopes and parameter values S_0, z, and τ of the power function STAR model (Eq. 3)

	SAC slope	Power function STAR model		
		S_0	z	τ
Taxon				
All Hymenoptera	0.45 ± 0.01***	73.0 ± 1.2***	0.41 ± 0.01***	0.09 ± 0.01***
Ichneumonidae	0.52 ± 0.02***	13.1 ± 1.0***	0.49 ± 0.01***	0.08 ± 0.03**
Braconidae	0.49 ± 0.02***	10.1 ± 0.7***	0.44 ± 0.02***	0.14 ± 0.04**
Chalcidoidea	0.41 ± 0.01***	20.7 ± 0.7***	0.39 ± 0.01***	0.05 ± 0.02*
Proctotrupoidea	0.45 ± 0.01***	8.7 ± 0.5***	0.43 ± 0.02***	0.06 ± 0.03(*)
Scelionoidea	0.43 ± 0.01***	5.7 ± 0.3***	0.39 ± 0.02***	0.07 ± 0.03**
Ceraphronoidea	0.35 ± 0.01***	7.7 ± 0.4***	0.28 ± 0.02***	0.17 ± 0.04***
Guild				
Miners	0.37 ± 0.01***	8.8 ± 0.5***	0.36 ± 0.02***	0.04 ± 0.04
Gall makers	0.41 ± 0.01***	9.5 ± 0.4***	0.38 ± 0.02***	0.07 ± 0.03 *
Ectophytophages	0.50 ± 0.02***	5.8 ± 0.4***	0.45 ± 0.02***	0.13 ± 0.04**
Sap suckers	0.34 ± 0.02***	6.0 ± 0.4***	0.22 ± 0.03***	0.23 ± 0.05 ***
Saprophages	0.38 ± 0.01***	9.7 ± 0.3***	0.35 ± 0.02***	0.07 ± 0.02**
Mycetophages	0.58 ± 0.02***	4.8 ± 0.3***	0.55 ± 0.02***	0.05 ± 0.04
Predators	0.35 ± 0.01***	7.8 ± 0.4***	0.31 ± 0.02***	0.07 ± 0.03**
Egg parasitoids	0.35 ± 0.02***	6.9 ± 0.4***	0.34 ± 0.02***	0.01 ± 0.04

(*) $P(t) < 0.1$; * $P(t) < 0.05$; ** $P(t) < 0.01$; *** $P(t) < 0.001$
Errors refer to standard errors

Table 3 Predicted annual species turnover rates (Eq. 3) of hymenopteran taxa and guilds

	Predicted annual species turnover
Taxon	
All Hymenoptera	7%***
Ichneumonidae	6%**
Braconidae	10%**
Chalcidoidea	4%*
Proctotrupoidea	4%(*)
Scelionoidea	5%**
Ceraphronoidea	13%***
Guild	
Miners	3%
Gall makers	5%*
Ectophytophages	9%**
Sap suckers	17%***
Saprophages	5%**
Mycetophages	4%
Predators	5%**
Egg parasitoids	1%

(*): $P(t) < 0.1$; * $P(t) < 0.05$; ** $P(t) < 0.01$; *** $P(t) < 0.001$

for the upper weight classes, rates of about 8% ($2^{0.11} = 1.079$).

In a fixed sample universe slopes and intercepts of SACs should be correlated (Gould 1979). Hence, the dependencies in Fig. 2 might result from lower species numbers per unit area in the upper weight classes. This was not the case. Neither z nor τ changed significantly with the predicted S_0-values per weight class regression (Fig. 3a, b). Instead, z and τ decreased significantly with mean density per species and weight class (Fig. 3c, d). This decrease might be connected with the well known negative density–body weight regression, which takes, for the forest Hymenoptera of this study, the form

$D = 0.12$ $W^{-0.50}$; $R^2 = 0.75$ (Ulrich 2004). A multiple regression, with log-transformed densities and body weights as predictors, pointed for both z and τ to mean density as the decisive predictor (density terms in both cases significant at $P < 0.01$; both regression weight terms > 0.1, data not shown).

The decrease of τ with increasing density is faster than that of z. The slope for z in Fig. 3c is -0.19, that for τ in Fig. 3d is -0.52. Hence the present STAR model infers a more pronounced effect of study time on species accumulation for hymenopteran species with lower mean densities.

Equation 3 assumes a power function STR. However, temporal species accumulation might also be linearly proportional to time ($S = S_t\,t$) or proportional to log (time) (in analogy to the logarithmic SAR model of Gleason 1922). Linear proportionality implies $\tau = 1$. However, the low τ-values of Table 2 do not corroborate linear proportionality. Fits of the STAR model with $\tau = 1$ had in all cases significantly lower R^2-values ($P < 0.01$) than those of the power function model (data not shown).

A logarithmic STAR model with a power function SAR term (Eq. 2) must have a study time term $f(t) = \alpha \ln(t) + 1$ to give unity for $t = 1$ (the simple SAR). Hence

$$S = S_0 A^z (\alpha \ln(t) + 1). \tag{6}$$

Figure 4 shows that this model was also able to predict study time and area corrected species numbers for all Hymenoptera. However, despite its high R^2 value of 0.98 the resulting SAR overestimated S_0 (81 ± 8.4 species) and underestimated species numbers for areas above 40 m^2 (66 out of 70 data points above the regression line). On the other hand, the study time parameter α did
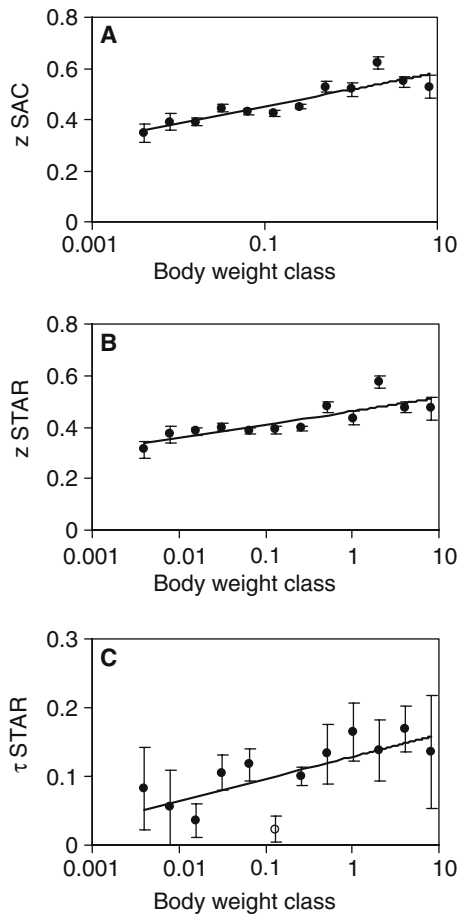
Fig. 2 a Dependence of simple SAC slope z on binary body weight class. **b, c** Dependences of STAR model slopes z and τ on binary body weight class. The lower body weight class (< 0.004 mg) was chosen as having at least 25 species per class. *Error bars* denote in all cases one standard error. Regression functions: **a** $z_{\text{SAC}} = 0.052$ ln(weight class) $+ 0.71$; $R^2 = 0.81$); **b** $z_{\text{STAR}} = 0.023$ ln(weight class) $+ 0.46$; $R^2 = 0.68$); **c** $\tau_{\text{STAR}} = 0.014$ ln(weight class) $+ 0.13$; $R^2 = 0.53$). Leaving the outliner (*open circle*) in **c** outside: $R^2 = 0.70$. All regression parameters are significant at $P < 0.001$. The *open circle* in **c** marks one outlier

not significantly differ from 0. In general, the logarithmic STAR model fitted worse ($R^2 = 0.83$; Fig. 4) than the respective power function model ($R^2 = 0.99$; Fig. 1). Similar results were obtained from pairwise comparisons of taxa and guilds. In 10 out of 14 single comparisons the power function SAR fitted better; in four cases both fits were nearly identical (data not shown).

Discussion

The above results show that it is possible to decompose a spatiotemporal process of species accumulation into its spatial and temporal components. This decomposition forms the basis for a general multiplicative species–time–area relationship. For the local community of Hymenoptera studied here, both the area and the time dependent model parts can be described by power

functions as predicted by Preston (1960) and reported by a few other studies (Rosenzweig 1995; Adler and Lauenroth 2003; White 2004; Adler et al.2005). Furthermore, Preston's conjecture silently implies that species numbers are proportional to the area and to the time function. Hence, the spatiotemporal accumulation should be proportional to the product of both terms. The present paper confirms this prediction and opens the way towards a general STAR model that incorporates time and area at different scales.

A potential complication of this result is that area and time are often correlated. In the present case, the sampling procedure implies that the largest sample areas above 80 m^2 are only obtained using the data from at least six of the study years. To overcome the problem of non-independence, Adler et al. (2005) applied a model in which area and time are not independent but multiplicatively connected. They added an additional parameter u to describe this interaction and proposed

$$S = S_0 A^{z+u \log t} t^{\tau+u \log A}. \tag{4}$$

A shortcoming of this model is surely that it involves an additional shape generating parameter that is ecologically weakly interpreted but makes model testing and verification more difficult. The four-parameter model incorporates the three-parameter model for $u = 0$ (Eq. 3) and is expected to fit all STAR shapes best (Gielis 2003). A fit of this model to the present data set resulted in ($R^2 = 0.99$)

$$S = (73 \pm 2) A^{(0.42 \pm 0.006) - (0.003 \pm 0.002) \ln(t)} t^{(0.11 \pm 0.016) - (0.003 \pm 0.002) \ln(A)}$$

$$\tag{5}$$

Hence, the parameter u appeared to be not significant at the 5% error level. The values of the parameters S_0, z, and τ remained largely unchanged (cf. Fig. 1). Therefore, I conclude that the interaction of area and time does not significantly influence the parameter estimates of the present STAR model. The present value of u is negative. Adler et al. (2005) also reported negative values of u in their analysis of various long-term data sets. They used Akaike information criterion to infer whether the interaction model is superior, but did not give significance values of their parameters. In the present case, the Akaike criterion points to the simple STAR model of Eq. 3 because both models fitted equally well (both $R^2 = 0.99$) and Eq. 4 contains one additional free parameter. Nevertheless, the contrasting results imply that researchers should always test for a possible interaction when applying a STAR model.

That the species time relationship might have a similar scale dependent triphasic form as the classical SAR has in part been shown by White (2004), who reported two-phase STRs for North American land birds. These two phases refer to small and medium time intervals, corresponding to ecological (< 5 years) and historical time scales. The present paper deals with the ecological time scale only.

Fig. 3 Dependence of z and τ of the STAR model on mean expected species numbers per square meter (S_0) (**a, b**) and mean densities per species (ind/m²/S) (**c, d**) per binary body weight class. Regression functions: **c** $z = 0.41$ (density)$^{-0.19}$; $R^2 = 0.62$; **d** $\tau = 0.10$ (density)$^{-0.52}$; $R^2 = 0.64$. All regression parameters are significant at $P < 0.005$
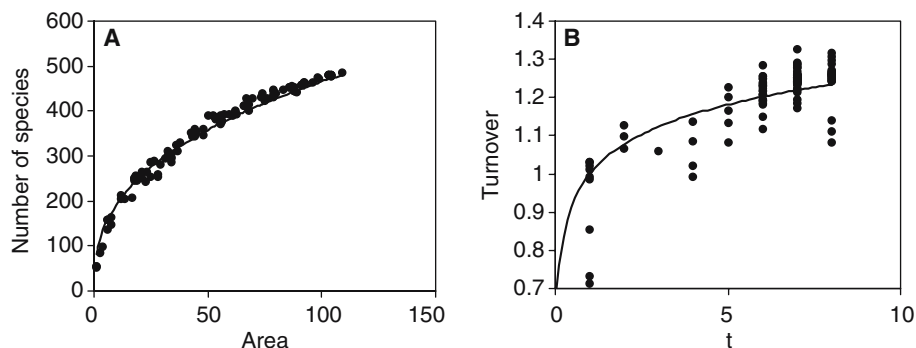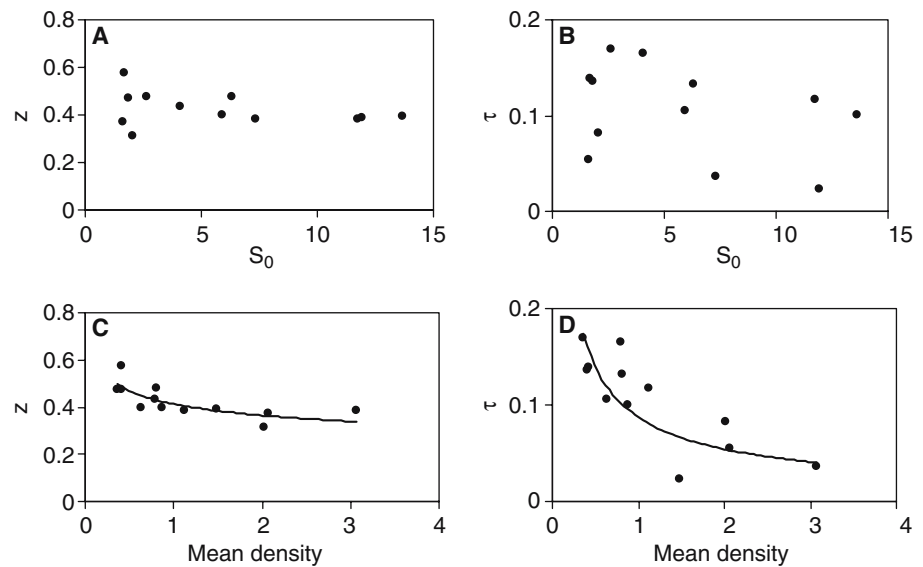

Fig. 4 a Fit of the power function SAR term of the logarithmic STAR model (Eq. 4) to the study time corrected species numbers [$S = (81.2 \pm 8.4)A^{(0.38 \pm 0.03)}$; $R^2 = 0.98$] **b** Fit of the logarithmic study time term of the same model to the area corrected species numbers (turnover) [$S = (0.11 \pm 0.07)\ln(t) + 1$]. The regression parameter does not significantly differ from 0 ($P = 0.10$). Complete STAR model: $R^2 = 0.83$

However, the regression slopes τ in the range from $\tau = 0.01$ to 0.23 with a mean of $\tau = 0.09$ (Table 2) are lower than the $\tau = 0.26$ predicted by Preston (1960) and $\tau = 0.19$–0.42 found by Adler and Lauenroth (2003), $\tau = 0.20$–1.00 by Adler et al. (2005), and $\tau_{second\ phase} = 0.16$ by White (2004). These studies dealt with regional to continental scales. STR slope values at local scales have not been reported yet. However, under the assumption that the STR of different taxa follows at local scales power functions, existing data of temporal species turnover and local extinction and immigration rates can be retransformed into STR slopes. Available data for local terrestrial and freshwater communities of arthropods point to annual turnover rates between 5% and more than 20% (Den Boer 1985; Harrison 1991; Hilpert 1989; Foley 1994; Arnott et al. 1999; Ulrich 2001a). Hence Eq. 3 predicts local arthropod STR slopes between $\ln(1.05)/\ln(2) = 0.07$ and $\ln(1.2)/\ln(2) = 0.26$. These predictions are similar to the slopes observed in this study. Contrasting results were, however, provided by Field et al. (2002) in a study of 'same-day' and 're-peated days' bird counts. Although they found an initial steeper SAC slope for repeated surveys the cumulative species numbers were independent of the time span the survey lasted ($\tau = 0$). This points to a rather closed bird community at the regional scale with limited species turnover.

The relatively high STR slopes of Adler and Lauenroth (2003), White (2004), and Adler et al. (2005) might indicate that τ increases with spatial scale. This would contrast to the SAR pattern where regional slopes are lower than local ones (Shmida and Wilson 1985; Rosenzweig 1995; Lomolino 2000; Storch et al. 2003). Furthermore, Adler et al. (2005) showed that, at regional scales, τ decreases with spatial scale in line with the lower SAR slopes. One might speculate that the spatiotemporal accumulation of species at local scales is dominated by spatial components due to small scale heterogeneity and sampling effects whereas at regional scales the temporal component due to dispersal becomes

more important. However, comparative studies to sustain this hypothesis are largely missing.

A time span of only 8 years is too short to compare fits by logarithmic and power function models in detail. Nevertheless, the above results (Figs. 1, 4) point at least at the local scale to a better fit of the power function STAR model, although the data do not allow for a strict testing of Preston's first conjecture. Unfortunately, this critique also applies to other recent tests of Preston's conjecture (Jacquemyn et al. 2001; Adler and Lauenroth 2003; White 2004; Adler et al. 2005) because a strict test would need much longer time scales. The power function STR shape is, however, well established at evolutionary time scales (Rosenzweig 1998; McKinney and Frederick 1999).

Temporal species turnover was significantly negatively correlated with mean density and positively correlated with body weight. That extinction risk as one part of temporal species turnover is indeed positively correlated with body weight has repeatedly been reported (Bennett and Owens 1997; Purvis et al. 2000; Ulrich 2001a; Gonzalez and Chaneton 2002). Under the assumption of fairly constant annual species numbers (Ulrich 2001b), local extinction has to be counterbalanced by immigration leading to a positive correlation between species turnover and body weight.

An unexpected finding was the strong positive correlation between SAR slope z and body weight. Because S_0 and z were not correlated this effect cannot simply be explained by the higher mean densities of smaller species leading to higher detection probabilities per unit area and therefore higher S_0-values. Nevertheless the most parsimonious explanation invokes lower encounter probabilities per sample of larger and therefore (in the mean) rarer species. At regional networks of habitat patches Biedermann (2003) recently reported a positive correlation between body size and the area–incidence relationship of terrestrial vertebrates and insects. Hence, occurrence probabilities per unit area should be higher for larger species and the relationship predicts lower slope values for larger species. However, a critical compilation of SAR patterns with respect to body size is still missing.

There is a long and ongoing debate about the slope values of SARs (Preston 1962; Connor and McCoy 1979; Sugihara 1981; Rosenzweig 1995; Rosenzweig and Ziv 1999). While most earlier authors argued that SAR slopes should scatter around 0.25 (Preston 1962; May 1975; Sugihara 1981), recent theories point rather to a wider range of slopes with island slopes being higher (> 0.2) than mainland slopes (0.05–0.2) (Rosenzweig 1995; Lomolino 2000). The present results have potential implications for the study of SAR slopes. Strictly, slopes should use point estimates of species numbers of different area size (Rosenzweig 1995). Instead, SARs that are based on data collected over longer time periods should contain an additional study time term. If we deal with a local scale and immigration occurs from a large species pool as in the present study, simple SAR slope values should be higher than the study time corrected SAR slopes. However, at larger scales with rather stable regional to continental species numbers, local species accumulation over time should lead to higher SAR intercept and lower slope values (Gould 1979). Hence, regional study time corrected SARs should have higher slopes than simple SARs. For example, a classical study of SARs is the work on butterfly species numbers of the West Indies (Munroe 1948). Munroe established species numbers for larger islands and inferred a SAR slope of 0.26 and an intercept of 0.8 species/km². Davies and Spencer Smith (1997) instead based their SAR of West Indies butterflies on the accumulated species records since 1948 and reported a slope of only 0.20 and an intercept of 1.06 species/km². Davies and Spencer Smith (1997) did not try to explain why they received a lower slope value, but this value and the higher intercept of their later study fits into the prediction of the present STAR model. The above example highlights the difficulties when comparing SAR parameter values obtained from repeated surveys. The present STAR model might become a tool for correcting simple SARs for study time and repeated survey effects.

References

Adler PB (2004) Neutral models fail to reproduce observed species-area and species time relationships in Kansas grasslands. Ecology 85:1265–1272

Adler PB, Laurenroth WK (2003) The power of time: spatiotemporal scaling of species diversity. Ecol Lett 6:749–756

Adler PB, White EP, Lauenroth WK, Kaufman DM, Rassweisler A, Rusak JA (2005) Evidence for a general species–time–area relationship. Ecology 86:2032–2039

Arnheius SE, Yan ND, Magnuson JJ, Frost TM (1999) Interannual variability and species turnover of crustacean zooplankton in Shield lakes. Can J Fish Aquat Sci 56:162–172

Arrhenius O (1921) Species and area. J Ecol 9:95–99

Bennett PM, Owen IPF (1997) Variation in extinction risk among birds: chance or evolutionary predisposition? Proc R Soc Lond B 264:401–408

Biedermann R (2003) Body size and area-incidence relationships: is there a general pattern? Global Ecol Biogeogr Lett 12:381–387

Carlson JM, Doyle J (1999) Highly optimized tolerance: a mechanism for power laws in designed systems. Phys Rev E 60:1412–1427

Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. Am Nat 113:791–833

Davies N, Spencer Smith D (1997) Munroe revisited: a survey of West Indian butterfly faunas and their species–area relationship. Global Ecol Biogeogr Lett 7:285–294

Den Boer PJ (1985) Fluctuations of density and survival of carabid populations. Oecologia 67:322–330

Field SA, Tyre AJ, Possingham HP (2002) Estimating bird species richness: how should repeat surveys be organized in time? Austral Ecol 27:624–629

Foley P (1994) Predicting extinction times from environmental stochasticity and carrying capacity. Conserv Biol 8:124–137

Fridley JD, Peet RK, Wentworth TR, White PS (2005) Connecting fine- and broad-scale species-area relationships of southeastern U.S. flora. Ecology 86:1172–1177

Funke W (1971) Food and energy turnover of leaf-eating insects and their influence on primary production. In: Ellenberg H (eds) Integrated experimental ecology. Ecological Studies 2. Springer, Berlin Heidelberg New York, pp 81–93

Gielis J (2003) A generic geometric transformation that unifies a wide range of natural and abstract shapes. Am J Bot 90:333–338

Gleason HA (1922) On the relation between species and area. Ecology 3:158–162

Gonzalez A, Chaneton EJ (2002) Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. J Anim Ecol 71:594–602

Gould SJ (1979) An allometric interpretation of species–area curves: the meaning of the coefficient. Am Nat 114:335–343

Hadley EA, Maurer BA (2001) Spatial and temporal patterns of species diversity in mountain mammal communities of western North America. Evol Ecol Res 3:477–486

Harrison S (1991) Local extinction in a metapopulation context: an empirical evaluation. Biol J Linn Soc 42:73–88

Harte J, Kinzig AP, Green J (1999) Self-similarity in the distribution and abundance of species. Science 284:334–336

Hilpert H (1989) Zur Hautflüglerfauna eines südbadischen Eichen-Hainbuchenmischwaldes. Spixiana 12:57–90

Hubbell SP (2001) The unified theory of biogeography and biodiversity. University Press, Princeton

Jacquemyn H, Butaye J, Hermy M (2001) Forest plant species richness in small, fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. J Biogeogr 28:801–812

Judas M (1988) The species–area relationship of European Lumbricidae (Annelida, Oligochaeta). Oecologia 76:579–587

Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. J Anim Ecol 70:966–979

Lomolino MV (2000) Ecologist's most general, yet protean pattern: the species–area relationship. J Biogeogr 27:17–26

Maurer BA, McGill BJ (2004) Neutral and non-neutral macroecology. Basic Appl Ecol 5: 413–422

May RM (1975) Patterns of species abundance and diversity. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Belknap, Cambridge, pp 81–120

McKinney ML, Frederick DL (1999) Species–time curves and population extremes: ecological patterns in the fossil record. Evol Ecol Res 1:641–650

Munroe EG (1948) The geographical distribution of butterflies in the West Indies. PhD Thesis, Cornell University, Ithaca

Preston FW (1948) The commonness and rarity of species. Ecology 29:254–283

Preston FW (1960) Time and space and the variation of species. Ecology 41:611–627

Preston FW (1962) The canonical distribution of commonness and rarity. Part I and II. Ecology 43:185–215, 410–432

Purvis A, Gittleman JL, Cowlishaw G, Mace GM (2000) Predicting extinction risk in declining species. Proc R Soc Lond B 267:1947–1952

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Rosenzweig ML (1998) Preston's ergodic conjecture: the accumulation of species in space and time. In: Mc Kinney ML, Drake JA (eds) Biodiversity dynamics: turnover of populations, taxa, and communities. Washington University Press, Madison, pp 311–348

Rosenzweig ML, Ziv Y (1999) The echo pattern of species diversity: pattern and processes. Ecography 22:614–628

Schaefer M (1996) Die Bodenfauna von Wäldern: Biodiversität in einem ökologischen System. Abh Math Naturwiss Klasse 2:1–81

Schaefer M (1999) The diversity of the fauna of two beech forests: some thoughts about possible mechanisms causing the observed patterns. In: Kratochwil A (ed) Biodiversity in ecosystems. Kluwer, Dordrecht, pp 45–64

Scheiner SM (2003) Six types of species–area curves. Global Ecol Biogeogr 12:441–447

Shmida A, Wilson MV (1985) Biological determinants of species diversity. J Biogeogr 12:1–20

StatSoft (2005) STATISTICA (data analysis software system), version 7.1. www.statsoft.com

Storch D, Sizling AL, Gaston KJ (2003) Geometry of the species–area relationship in Central European birds: testing the mechanism. J Anim Ecol 72:509–519

Sugihara G (1981) $S = CA^z$, $z \approx 0.25$; a reply to Connor and McCoy. Am Nat 117:790–793

Tjørve E (2003) Shapes and functions of species - area curves: a review of possible models. J Biogeogr 30:827–835

Ulrich W (1998) The parasitic Hymenoptera in a beech forest on limestone I: species composition, species turnover, abundance and biomass. Pol J Ecol 46:261–289

Ulrich W (1999a) Regional and local faunas of Hymenoptera. Pol J Entomol 68:217–230

Ulrich W (1999b) Temporal stability of community structure of the parasitic Hymenoptera in a beech forest on limestone. Pol J Ecol 47:257–270

Ulrich W (2001a) Differences in temporal variability and extinction probabilities between species of guilds of parasitic Hymenoptera. Pol J Entomol 70:9–30

Ulrich W (2001b) Hymenopteren in einem Kalkbuchenwald: Eine Modellgruppe zur Untersuchung von Tiergemeinschaften und ökologischen Raum-Zeit-Mustern. Schriftenr Forschzentr Waldökosyst A 171:1–249

Ulrich W (2004) Allometric ecological distributions in a local community of Hymenoptera. Acta Oecol 25:179–186

Ulrich W, Buszko J (2003a) Species–area relationships of butterflies in Europe and species richness forecasting. Ecography 26:365–374

Ulrich W, Buszko J (2003b) Self-similarity and the species - area relation of Polish butterflies. Basic Appl Ecol 4:263–270

Ulrich W, Ollik M (2004) Frequent and occasional species and the shape of relative abundance distributions. Div Distr 10:263–269

White EP (2004) Two phase species - time relationships in North American landbirds. Ecol Lett 7:329–336

Williamson M (1988) Relationship of species number to area, distance and other variables. In: Myers AA, Giller PS (eds) Analytical biogeography. Chapman & Hall, New York, pp 91–115